
ONE HUNDRED YEARS OF PLANT TAXONOMY, 1889–1989¹

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ABSTRACT

One hundred years ago taxonomic botany was at the end of the first phase of producing great regional floras and encyclopedic compendiums, especially with the work of George Bentham and Joseph Hooker in Britain, Asa Gray in the U.S.A., and Alphonse de Candolle in Switzerland. The vast influx of new botanical discoveries from exploration had highlighted interest in biogeography, interpreted in terms of new evolutionary insights. The subject had been in high regard and major herbaria had recently been founded. A widespread decline of activity and prestige followed, when emphasis shifted to other botanical fields, except in Germany where Adolf Engler further developed encyclopedic coverage of plant families and genera worldwide. Revival of biological taxonomy came slowly through genetics to the “new systematics.” Karyology, biosystematics, phytochemistry, and comparison of isozymes were in turn seen as panaceas; each failed to meet these expectations but continues to contribute as part of the armory of relevant approaches. Emphasis on methods of analysis led to the decade of numerical phenetics. Partly from lack of a satisfactory theoretical basis, phenetics came to be widely rejected but gave place to cladistics, ranging from the avowedly phylogenetic to abstract pattern analysis. Macromolecular genetics with analysis of data from nuclear, ribosomal, mitochondrial, and especially chloroplast genes is now rapidly producing robust data to address many previously intractable problems at all taxonomic levels by selection of appropriate gene systems. Such data may produce convincing phylogenetic trees without input from morphology, leading some to question whether systematic botany remains “an unending synthesis,” though warnings against overconfidence have been sounded both from aspects of gene systems and from the way the data are analyzed. A challenge is to maintain cohesion in systematics so that the new developments are a scientific stimulus to the subject as a whole and so that herbaria and other institutions concerned with floristic projects remain within the mainstream of scientific taxonomy. Insofar as macromolecular systematics lives up to its early promise, the task of systematics may eventually become, in part, the interpretation of morphology and evolution in terms of highly corroborated phylogenies—a synthesis on new terms. As well as these more theoretical approaches, providing organized information on the diversity of the world’s plants through national and regional floras remains a priority.

A brief paper cannot adequately review a century of work by taxonomists, who were numbered in tens a century ago and who are now in thousands. Their work filled our herbaria with specimens and our libraries with publications. This whirlwind tour places emphasis on the beginning and end of our time frame, and gives least attention to those fields where my lack of expertise would otherwise be most conspicuous. Two other limitations will be apparent. The extent of emphasis on work in the English-speaking countries and on seed plants alone is justified by my greater familiarity with those areas.

AN UNENDING SYNTHESIS?

With this eloquent and much-quoted phrase Lincoln Constance (1964) characterized the nature of systematics—a term that I use in part inter-

changeably with taxonomy (in general agreement with Small [1989] in the use of these terms). Modern macromolecular genetics has contributed such powerful tools to taxonomy that Gottlieb (1988) queried whether this characterization was still appropriate, and I will return later to this question. Traditionally, data from many fields have been grist for the mill of taxonomy. So this subject has reason to be responsive to developments in science generally, as well as profiting from technological advances that increase its power to assemble and organize relevant data. This responsiveness has been and remains a two-way process. Taxonomy has given the basis for one of the greatest unifying concepts in science—evolution—since it is taxonomy that has the main task of making accessible our organized knowledge of the patterns of diversity of living things.

A hundred years ago the scientific context for

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taxonomy was the result of a century of dramatic progress (e.g., Taton, 1965). Since the start of the nineteenth century there had been:

- the acceptance of atomic theory with insight into molecular structure and chemical reactivity;
- bacteriology with the inception of scientific medicine;
- the interpretation of geological structures, with the international geological scale of epochs and periods replacing “catastrophic” models of the earth’s past;
- the beginning of understanding of the structure of organisms in terms of cells, nuclei, cell division, and life cycles;
- and then, most dramatic in modifying general thought, had been the concept of biological evolution.

Still lacking were:

- extension of the limits of knowledge of the universe in its largest extent that would come with modern astronomy and cosmology and in its fine detail extending from modern microscopy to quantum physics;
- modern philosophy of science with sharper focus on falsifiability of hypotheses;
- systems theory and now chaos theory;
- sophisticated concepts of energy, matter, and their range of manifestations and transformations in physical and biological systems;
- plate tectonics and the history of continental movements and paleoclimatology;
- the localization of genetic inheritance largely to chromosomes, with concepts of genes and mechanisms of heredity;
- classification and definition of the major categories of organisms beyond simplistic groupings into plants, animals, and fungi;
- the symbiotic theory of the eukaryotic cell;
- technical advances in all fields, including chemical analysis, microscopy, computing, and communication;
- extension of centers of scientific research and teaching beyond the limits of Europe and North America.

END OF AN ERA

A century ago Charles Darwin had been dead seven years and the appearance of *The Origin of Species* was 30 years into the past. What scientist then would have thought that evolution (as distinct from ‘Darwinism’) would still be a contentious issue,

still needing to be defended in some circles although not within science, a hundred years into the future? Within science it is evidence of Darwin’s importance that his work still attracts critics today, but mostly their concerns are with the nature of the evolutionary process and the way it is described, rather than denying evolution itself.

In the previous century, before 1889, exploring parties in many regions had been gathering specimens of unfamiliar plants, still bringing them to the seats of learning in the temperate northern hemisphere, rather than expecting or seeking to establish expertise distributed worldwide. This pace of botanical exploration and interest in joining expeditions continued to be powerful stimuli in attracting active minds to taxonomic biology, as they had been in the time of Charles Darwin and earlier.

By 1889 taxonomy was at the end of the first round of great regional floras and encyclopedic treatments of the world’s plant taxa. George Bentham had died in 1884 and Asa Gray in 1888, although Alphonse de Candolle was still alive and Joseph Hooker would continue publishing for another 22 years till 1911. The importance of these botanists and their work is such that we should extend our time frame back a little to consider them all. Indeed, by going back to September 1880 we could have looked in on any of several little dinner gatherings in the director’s house at Kew Gardens near London and found all four of them together (J. Gray, 1893). These were all old friends, old in years and who had met many times before, but think of what a prodigious botanical output is represented here.

First the host to these gatherings, Joseph Hooker. Dr. Hooker was for 20 years director of the Royal Botanic Gardens, Kew, London and spent a long active retirement, his last botanical paper being published in the year of his death at the age of 94 (Allan, 1967; Bower, 1919). He had made notable travels in the southern continents, in India, and high into the Himalayas. The *Flora of British India* and *Genera Plantarum* were joint with George Bentham, who took the greater share, but major essays on plant geography were his alone. The incisive, wide-ranging phytogeographical assessments in his discussion of southern hemisphere plant distributions (Hooker, 1859) were only set aside when modern plate tectonics gave a new framework for interpreting plant geography. Joseph Hooker had played a major part in encouraging Charles Darwin and had been Darwin’s closest confidant and first supporter.

Next there is Bentham, known to his associates as a prodigious worker (Jackson, 1906), who had

published a wealth of critical treatments of particular families as well as the *Flora Hongkongensis* and the *Handbook of the British Flora*. His *Flora Australiensis* had been 16 years in preparation, but during those years he had been pressing on also with the mighty *Genera Plantarum*, jointly with Hooker. His botanical judgments have stood well, but subsequent authors have too often simply used Bentham's classifications and ignored his comments that indicate how often decisions were tentative, as seen by himself, and influenced by the limited information available at the time.

Alphonse de Candolle brings yet another strand. He had succeeded his father, Augustin-Pyramus de Candolle (A. P. de Candolle), as professor and director of the botanic garden at Geneva, and also inherited responsibility for the *Prodromus* (A. P. de Candolle, 1824 et seq.). This work attempted a systematic treatment of the world's dicotyledons down to the level of species and variety. The elder de Candolle had turned away from the artificiality of the Linnean system and attempted to apply the modern principles of his time, and his son had reinforced this trend. The *Prodromus* set standards of format and nomenclature that became increasingly widely adopted. After taking over the half-completed work, with only seven of the eventual 17 volumes published, Alphonse made the work more international and better-based through seeking external collaborators, by visiting other herbaria, and through extensive loans of specimens. His publication *La Phytographie* became a standard work on the principles of plant taxonomy, and he had a leading part in the first codification of botanical nomenclature (A. de Candolle, 1867).

Then there was Asa Gray. He had collaborated with John Torrey on *The Flora of North America* (Torrey & Gray, 1838–1843) and later had published widely on the plants and phytogeography of North America and also their relations with the flora of Japan. A notable teacher, he had produced a range of important textbooks, inspired a stream of outstanding botanists, and founded the Harvard herbarium that bears his name. Himself a systematist, he also encouraged students into other disciplines and was conscious of the value and importance of morphology, anatomy, and physiology.

A TIME OF CHANGE, A CENTURY AGO

BOTANY AS A SCIENTIFIC CAREER

The careers and work of these four botanists emphasized changes that were already in evidence and that would set the scene for the future. Botany in the nineteenth century had been both burdened

and blessed by being adopted as a socially desirable genteel pursuit for the newly wealthy, and one that combined well with the romantic idealism of the time (Scourse, 1983). This fashion grew as a corollary to increasing industrialization and urbanization and gave the subject some problem in establishing its scientific credentials. But for our group of botanists there was no doubt: their motivation and careers had been scientific.

Hooker and Gray had originally studied medicine, thus receiving some formal botanical training; Bentham and de Candolle had taken law. Two had learned much of their botany assisting distinguished fathers, whereas Gray had worked with John Torrey at New York. We see here two types of botanical inheritance.

Gray received from Torrey inspiration and knowledge and in turn passed this on in equal measure to his many students. The age of the teacher and student was replacing that of the master with his assistant. It was now the time of the professional scientific career. Bentham seemed to regard himself as something of an amateur even when he had major achievements to his name, in contrast to Dr. Hooker and others formally trained in botany. Also, Bentham alone of this group had continued the earlier tradition of the unpaid scholar, having a modest inheritance and "finding . . . that I need not toil for our support [he observes], I determined to give up the law and devote myself entirely to botany" (Jackson, 1906).

THE GROWTH OF COLLECTIONS AND INSTITUTIONS

When William Hooker was appointed as director of Kew Gardens in 1841 it had neither herbarium nor library and was essentially a pleasure garden (Hepper, 1982). He left it as the scientific institution that his son Joseph continued to develop. The original nucleus of the Kew herbarium was William Hooker's personal collection, purchased on his death by the British government (Blunt, 1978; Desmond, 1975). Its library also started with William Hooker's own books, much augmented when Bentham offered his library of 1,000 volumes; Bentham made only the condition that he be allowed to use it there (King, 1985).

That most useful, if simplest, of resources for the taxonomic botanist—the herbarium specimen—already had a long history, but large herbaria were recent developments. The foundation of London's Kew herbarium is dated as 1853, and collections were building up in St. Louis, at Harvard University, and elsewhere. But many other

major herbaria, for example in New York and Chicago, were still in the future. Much of the early contact among botanists arose through requests to collect or identify specimens, as for example Asa Gray's early dealings with John Torrey and later with George Engelmann (J. Gray, 1893; Humphrey, 1961). Now that there are large herbaria of worldwide scope widely distributed, it is hard to equal the enthusiasm with which these botanists awaited and received new consignments of specimens from distant lands.

None of these four great men had successors of comparable standing. Geneva continued as an important botanical center but never again rivaled its place in the time of the de Candolles. Similarly, after the death of Asa Gray, no individual has dominated the American botanical scene as he had (Ewan, 1969; Heiser, 1969), although important successors included Charles Bessey, notable for his attempt at a phylogenetic system of flowering plant classification, and Liberty Hyde Bailey, with his unrivaled works on cultivated plants.

Under the two generations of Hookers, Kew developed exchange, especially in plants of potential economic value, with the British colonies, and Kew directors determined the control of colonial botanical gardens. Under its next director, Thistleton-Dyer, with the British Empire at its peak, economic botany came to dominate much of Kew's work and influence (Brockway, 1979). Kew continued as an outstanding center of botanical resources, but no longer held the lead in botanical research.

DEVELOPMENT OF BOTANICAL PROCEDURES AND COOPERATION

Standardized formats and procedures for plant description, specimen citation, and reference had developed early. Works from this time therefore have formats relatively little different from many modern works. Indeed, some standard conventions in botany seem to be vestigial and probably regrettable survivors from this age when the subject was in the hands of a small group of botanists well known to one another. This applies to some of the conventions for the citation of botanical authorities and brief reference to publications in taxonomic treatments. In the formalization of botanical presentation, both descriptive and nomenclatural, all these leading botanists had set standards that were followed long into the future (Frodin, 1984).

Our group of notables had also orchestrated much of the labors of a farflung band of associates who strove to assist, in return for encouragement

and approval. Among them had been Ferdinand von Mueller in Melbourne (Willis, 1949), William Harvey in Cape Town (Ducker, 1988), and Engelmann in St. Louis. All were productive in their own right, but also contributed importantly to joint works or resources available to Bentham, Hooker, or Gray. In the *Prodromus*, de Candolle had coordinated the work of 35 botanists in eight European countries (Stafleu, 1966). A comparable degree of wide cooperation on international projects is only now being rekindled and is made easier by such organizations as the International Association of Plant Taxonomists (Stafleu, 1988), as well as by modern technology.

EVOLUTION

Each of these botanists had taken up the new evolutionary thinking. Hooker, Gray, and de Candolle had used it as a basis for discussions of phytogeography and had been especially active in promoting its acceptance. Yet the system adopted in Bentham and Hooker's *Genera Plantarum* was modeled closely on that of the pre-Darwinian Augustin-Pyramus de Candolle. As Stevens (1984) has pointed out, the incorporation of the evolutionary time-axis and concepts of divergent evolution had remarkably little effect on the classifications they produced, which were often reminiscent of earlier ideas of a network of living organisms.

THE BERLIN SCHOOL

The next major botanical phase was not a direct legacy from any of our four botanists. The focus shifted to Germany, where the German universities had been preeminent for some decades in research on plant structure, developmental morphology, and physiology, as well as providing training to many students from other countries including the United States. This continued with rigorous morphological interpretation, static in some aspects, but with valuable precision of analysis. Adolf Engler had been appointed in 1889 as professor and director of the botanical garden in Berlin. There, and previously at Breslau (now Wroclaw) and in his general approach, Engler followed in the steps of his mentor August Eichler, but with vastly expanded aims (Stapf, 1930). Engler's name "symbolizes the spectacular development of German botanical systematics in the late nineteenth and early twentieth century" (Stafleu, 1972), and his *Syllabus* (1892) has been followed by much advanced and very useful further editions up to recent times (Melchior, 1964). The *Pflanzenfamilien* (Engler & Prantl, 1887–1915) and *Pflanzenreich* (Engler, 1900–

1953) have been the last of the great encyclopedic treatments of the plant kingdom. These projects, envisioned by Engler and assisted by Prantl and many others, continued for decades on much the original plan. Only when the current project of Kubitzki and others (Bates et al., 1980) comes to fruition will their status be challenged.

Engler's attempt to arrange plant orders and families in what he conceived to be phylogenetically determined sequences was only partly successful since it did not recognize the extent of reduction trends that produced structurally similar forms.

DECLINE AND RISE

Encyclopedic projects such as Engler's, however vast their scope and achievement, were assembling existing knowledge rather than moving ahead in scientific concepts or methodology. By now the rush of exotic discoveries had lost impact and the physical sciences and biochemistry were on the rise. In both botany and zoology, taxonomy was in decline before the end of the nineteenth century and was seen as a scientific backwater, unattractive to the best minds. Botanical taxonomy was continuing the task of cataloging and naming the world's plants, with more emphasis than before on the cryptogamic groups. Around the world the general rate at which herbaria were founded (Ma, 1988) was increasing almost exponentially, but this was not an indication of the scientific standing of herbaria.

Rollins (1965) expressed it well: near the end of last century "herbaria were respected centres of teaching and research. The most eminent men of botany were associated with them." By contrast, over some decades up to the middle of the present century, "Having established its place in the University and in the Museum, the herbarium attracted less venturesome scholars, who narrowed the dimension of their activities . . . the image became one that reflected stultification, diffidence and rigidity without sinews to bind it to the main stream of biological teaching and research."

Taxonomy would be revitalized a few decades later from a source that was already at hand early in the present century—the new field of genetics. Hull (1988) recounts how several workers around 1900 independently experimenting on character segregation came upon Gregor Mendel's publications. Soon genetics was a flourishing experimental and theoretical field, but at first genetics was seen to be incompatible with and opposed to Darwinian evolution. The reconciliation and fusion of genetics and evolution came when Fisher, Hal-

dane, and Wright began to develop concepts of the structure and dynamics of populations, and Darlington (1937) expressed the relevance of genetics to plant evolution.

The integration of genetics with evolutionary biology at the taxon level came later with the "new systematics," which was led by zoologists Dobzhansky, Simpson, Mayr, and Huxley, but which affected all systematic biology.

NEW DATA SOURCES OR PANACEAS?

The rediscovery of Mendel's work was followed by the identification of chromosomes as genetic material and the realization that chromosome morphology offered characters for study.

Moreover, karyology sometimes suggested hypotheses about processes and directions of evolutionary change, although these were often hedged with statements that certain directions were "unlikely" rather than "excluded from consideration." Early work was summarized in *Variation and Evolution in Plants* by Stebbins (1950), which helped to inspire a generation of research students of my time, as Darlington (1937, 1939) had done for our mentors in this field. Applications of karyology were numerous at all levels, from infraspecific to considerations of base numbers and major trends for orders and families and for the angiosperms themselves (Raven, 1975). The extent and patterns of chromosomal variation led students of phylogeny to mistrust or downgrade the importance of chromosomal information for broad considerations (Raven, 1975), but such information has thrown important light on relationships and processes in many groups (Moore, 1978).

Along with chromosomal studies in the early decades of this century went biosystematics. This field seems to have been variously defined, certainly embracing studies of variation, population structure, and breeding systems, but at other times taking in karyology, cytogenetics, and the whole of genic molecular evolution (Grant, 1984; Vickery, 1984). In line with biosystematic thinking, taxonomists for decades sought justification of their categories from biological species concepts. Ehrlich & Raven (1969), Raven (1977, 1980), and others have shown that much that has been claimed about species as interbreeding populations does not accord with the situation in nature. They pointed out how limited the gene flow is between the distant local populations of a widespread species, but that members of such a species are held together by common ecological constraints. It is scarcely an elegant solution that the term "species" is now

concurrently applied to various different concepts, but at least some consensus seems to have been reached in botany (e.g., Davis & Heywood, 1963; Raven, 1976, 1986; V. Grant, 1981; W. Grant, 1984; Haufler, 1989) so that semantics no longer dominates over observations on the situation in nature. In general, biosystematics, at least as narrowly defined, seems to have contributed less to taxonomy than to understanding evolutionary processes and part of its field has been claimed by its vigorous offspring, pollination ecology. It remains a useful approach in its own right but somewhat separate from the main thrust of taxonomy.

Alston & Turner (1963) characterized the first half of this century as the cytogenetical phase of systematic biology, whereas they designated 1950 onward as the biochemical phase. Twenty years later Harborne & Turner (1984) made a more modest claim, stating that they did "not believe that biochemistry represents a panacea for all systematic problems" and indeed that the role of systematics as a framework for the ordered arrangement of observations applies as well for biochemical data as for morphology. Secondary metabolites have proved their use, and compendiums such as Hegnauer's (1962–1973) have a wealth of data, especially for studies at higher taxonomic levels. Indeed, the strength of Dahlgren's system of the flowering plants (1980) lies mostly in placing greater emphasis on chemical characters than do other modern systems. So far, the chemical data have generally supplemented morphological data rather than replacing them. The first biochemical phase of taxonomy seems to have largely bypassed the majority of taxonomic practitioners until now. Remaining oblivious to the macromolecular phase will not be so easy.

In respect to systematics, both cytogenetics as envisaged early this century and chemosystematics failed to fulfill their early promises, but they have found their place as valuable aspects of multidisciplinary taxonomy. Perhaps one of the surprises has been the resurgence of morphology.

The basis of early classifications was exomorphology, but the range of relevant structural aspects has been greatly widened as means of observation improved and as concepts of homology have been more strictly applied. Thus that excellent symposium "The Bases of Angiosperm Phylogeny" (Walker et al., 1975) included structural topics ranging from floral or vegetative anatomy and morphology to palynology, embryology, and ultrastructure. The new findings have been especially rewarding at the upper taxonomic levels, as with

structure of leaf teeth (Hickey & Wolf, 1975) or the ultrastructure of sieve-element plastids (Behnke, 1975).

A related advance has been the integration of critical morphology with cladistic and biogeographic approaches into botanical palentology (e.g., Crepet & Nixon, 1989). A better explored fossil record, with more precise morphological observation and comparison, is throwing more light on the interpretation of living groups (e.g., Dahlgren, 1983).

EMPHASIS ON ANALYSIS, PHENETIC AND CLADISTIC

Many biologists were well pleased to be working with these expanding fields of data but others looked to new possibilities of making systematics more objective through attention to the philosophy and practice of data analysis. The early converts to these numerical methods seemed to find their satisfaction more in methodology than in improving knowledge and classifications of organisms.

In retrospect, numerical phenetics based on exomorphology seems something of an aberration and its theoretical basis (or lack of it) was much criticized at the time (e.g., Mayr, 1965; Johnson, 1968, 1970). But it held centerstage in both zoological and botanical taxonomy during the 1960s into the 1970s, and the major expositions of this approach were much followed (Davis & Heywood, 1963; Sokal & Sneath, 1965; Sneath & Sokal, 1973).

Hull (1988: 130) gives graphic expression to the next turning point:

"In the hubbub over numerical taxonomy, hardly anyone noticed scurrying around in the underbrush the ancestors of the next dominant group in systematics, as inconspicuous and active as the progenitors of the mammals had been in the age of the Dinosaurs."

Cladistics as an established approach dates from the "discovery" by Kiriakoff and others of the work of Willi Hennig (Hennig, 1950, 1966), although numerical methods to elucidate phylogenetic lineages based on synapomorphies were independently developed around that time or soon after by others (e.g., Wagner, 1961; Camin & Sokal, 1965; Johnson & Briggs, 1975). In his comprehensive account of the development of cladistics, Hull aptly describes Hennig's contribution:

"The methods he described for reconstructing phylogeny were not especially new. Rather his chief contribution was the clarity with which he set out his principles and the emphasis he placed on them."

Since then, cladistics has presented an exceptionally argumentative scene as it challenged the survivors of the "New Systematics"—great phylogenists like Mayr and Simpson. Cladistics has sharpened taxonomic thinking and brought emphasis back to the evolutionary basis of nature's hierarchical patterns (e.g., Eldredge & Cracraft, 1980; Wiley, 1981; Nelson & Platnick, 1981; Farris, 1983; and the greater part of the contents of *Systematic Zoology* for more than a decade). Even so, many cladists (pattern cladists) sought to make their analyses as theory-free as possible, to separate the analysis from any theoretical explanation that might be used to interpret it.

Guiding principles have been monophyly or holophyly, use of outgroups or hypothetical ancestors, and parsimony. Similarity in plesiomorphous features is dismissed as irrelevant, and grouping into clades depends on synapomorphies alone. Some practitioners seem to forget that evolution is not necessarily parsimonious but rather that the choice of the shortest tree, with fewest steps from the common ancestor to the member taxa, depends on a philosophical approach that excludes uncorroborated suppositions and unnecessary steps not decreed by the data. The evaluation of character homology has led to much desirable reinterpretation of the morphological and developmental equivalence of features. Methods differ in whether they accept trend reversals or work under a restricted parsimony model. Important concerns are falsifiability of hypotheses, and the writings of Karl Popper and other philosophers are much quoted.

Cladists have exaggerated the extent of innovation in their approach (Ghiselin, 1984) and have often been overconfident about their results. Misleading and ill-based conclusions can come from misinterpretation of homology, lack of commensurability or balance in the characters selected, extensive parallelism, or from methods that do not show the full extent of competing trees of equal or near-equal length. Such problems are now being addressed by more critical assessments, improved methods (e.g., PAUP, Swofford, 1985), and concentration on "robustness" with consensus trees and "bootstrap" or "jack knife" procedures.

Practical difficulties arise from paraphyly (Cronquist, 1987; Johnson, 1989) and bear consideration. When paraphyly is well corroborated it is often appropriate to accept a new classification based on cladistic analysis. But, for instance, should one fail to give taxonomic recognition to a well-marked group (one that is itself holophyletic) on the grounds that it leaves a paraphyletic residue

that is not yet resolved? Perhaps classifications may include both monophyletic and paraphyletic groups, with those that are not monophyletic clearly identified as such (as suggested by Wiley, 1981).

Cladistics has been justified on the grounds that "truth emerges more readily from error than from confusion. Perhaps [Hennig's] phylogenetic systematics might prove to be mistaken, but no one was going to be able to accuse it of being confused" (Hull, 1988), and cladistics has been tagged "cladistics: being wrong **with confidence**" (Penny et al., 1990); these judgments carry a valid warning but not a reason to reject cladistics. It has proven its power, and almost any issue of a modern systematic journal will show it as the method of preference for intensive investigations of plant groups at all levels. Noncladistic similarity methods are, however, widely but not unanimously advocated for analyzing macromolecular sequence data, as mentioned below.

Cladistics also concentrated attention on another problem: if a genealogical tree has been established, how should the categories of the taxonomic hierarchy be assigned to its branches? Major categories tend to be claimed by the divergence of groups at the base of the tree, leaving minor categories to assign to the most diverse and prominent groups. Thus, in the system of Bremer (1985) the flowering plants form subclass Magnoliidae within the Chlorobionta, whereas the Anthocerotatae are a superclass. This has logic, concentrates awareness on important new understanding, and is probably the way of the future. There is, however, some loss in communication as well as some gain: people are interested in "grade" aspects of organisms and their adaptive syndromes, as well as in their genealogies. Terms like 'amphibians' and 'reptiles' have conveyed information on levels of organization, even if we now find that they refer to paraphyletic assemblages.

MACROMOLECULAR BIOLOGY

Cladistics swept through systematics as something of a revolution little more than ten years ago. Already a new turning point is at hand—the application of macromolecular genetics to systematics.

Isozymes, the first manifestation of this approach, made their appearance in taxonomy in the 1960s. Some early workers on isozymes have since led the charge into nucleic acid studies, but isozymes continue to have a place, especially in work at the lower taxonomic levels including investiga-

tions of population variation (Crawford, 1983; Giannasi & Crawford, 1986; Ferguson, 1988; Brown, 1990). Isozymes sample only nuclear genes that are expressed as enzymic or structural proteins (Clegg et al., 1984), and exclude genes from other organelles.

Next came amino-acid sequencing of proteins, which has been described (Giannasi & Crawford, 1986) as "an approach whose time has come and gone (with regard to *plant* phylogeny) during the past two decades." Such sequencing has contributed importantly to phylogenetics of flowering plants at higher taxonomic levels (e.g., Boulter, 1973; Martin & Dowd, 1990). But proteins show many parallel base substitutions and this gives rise to distortions in their use to interpret phylogeny (Boulter, 1980).

Present emphasis is on base-sequencing of genomes. Genomes offer a large number of potential characters for study (Ritland & Clegg, 1987). They also have advantages of universality exceeding any morphological characters and approached only by a few cytological features. Some gene systems have been so conservative that all living things from the level of bacteria include homologous genes (e.g., those coding for hemoglobins, Appleby et al., 1990). Other gene systems have been quite labile and show differences between allied species or between individuals within a population (Clegg et al., 1984; Jorgensen & Cluster, 1988). Noncoding regions may provide data complementary to those from protein-coding regions since they are subject to different functional constraints (Zurawski & Clegg, 1987; Clegg, 1989).

The technical difficulties in obtaining data are being overcome, so that information is available from chromosomal, mitochondrial, and chloroplast genomes. Chloroplast DNA analysis provides data with exceptionally low levels of homoplasy, relevant to the time frame of the evolution of significant groups of flowering plants, and that lead to robust trees. Mitochondrial DNA is more variable in structure and organization in plants than is chloroplast DNA, and recombinant types arise in hybrids, whereas chloroplasts are strictly maternally inherited in most flowering plant groups. Ribosomal RNA contains both highly conserved and variable regions and so is useful over a wide time range (Baverstock & Johnson, 1990).

A notable example of informative restriction site analysis of chloroplast DNA is in the Asteraceae. The distribution of a large inversion suggests that the initial dichotomy was the separation of subtribe Barnadesiinae (Mutisieae) from the rest of Asteraceae, including from the three other subtribes of

the Mutisieae (Jansen & Palmer, 1987, 1988; Bremer, 1987; Palmer et al., 1988).

The pace has accelerated in the last few years with important data coming from Fabaceae (Doyle, 1987; Doyle et al., 1990), Onagraceae (Gottlieb, 1988; Sytsma & Smith, 1988), Poaceae (Hamby & Zimmer, 1988), and various groups (Palmer, 1987; Palmer et al., 1988) including Caryophyllales, Orchidaceae, Solanaceae, Fabaceae, and studies within the genus *Brassica*.

The living collections of botanical gardens are coming into their own as accessible research material for macromolecular work, but the technology can now use minute amounts of nucleic acids so that herbarium specimens can serve as sources for enzymes for electrophoresis (Ranker & Werth, 1986) or for DNA (Doyle & Dickson, 1987), and even the partially degraded material of some fossils can give information (Paabo, 1989).

The data are voluminous even when only a few gene systems are investigated. If methods of numerical analysis were not already accepted procedures in systematics, they would have had to be invented now to cope with this flood of new data. The power and relevance of the macromolecular data are clear, but warnings against excessive confidence have been sounded. Penny et al. (1987, 1990) draw attention to problems arising when data are insufficient, not representative of the genome as a whole, or when methods of analysis lead to convergence on an incorrect tree (including cases where a tree is not an appropriate model).

Studies of chloroplast or mitochondrial DNA are elucidating the phylogeny of organelles, not directly that of the organisms that contain them. Thus the gene phylogeny may depart from the species phylogeny. For instance, maternal inheritance of mitochondria in higher animals (Neigel & Avise, 1986) produces anomalous results in comparisons of conspecific individuals and recently diverged species. As a result, the phylogenetic distribution of mtDNA may not be concordant with species boundaries. As mentioned above, chloroplasts are also strictly maternally inherited in most flowering plant groups.

Methods of analyzing molecular data have rightly generated much discussion. A two-step procedure with cladistic methods to produce trees and maximum-likelihood similarity methods to evaluate those trees (Templeton, 1983) appears to have advantages. Farris (1985) and Cracraft (1989) have called for cladistic methods to be used more generally with sequence data, but others have pointed to problems that may arise in parsimony analyses (e.g., Felsenstein, 1978; Jansen & Palmer, 1988).

MAJOR GROUPS AND THEIR RELATIONSHIPS

Cladistic studies within orders or large families have tended to show few synapomorphies marking the lower internodes of early-divergent clades, so that some or all of the major groupings are not robust (e.g., Myrtales and Myrtaceae—Johnson & Briggs, 1984; Rosaceae—Kalkman, 1988; Caesalpinioideae, the basal group within the legumes [lack of robust groups is clear from descriptive comment—Polhill & Vidal, 1981—rather than from formal cladistic analysis]). The hypotheses represented by competing trees in such analyses have nevertheless led to marked improvements on earlier views of relationships. Even more improvement toward robust phylogenies can be expected where such analysis has available macromolecular markers relevant to subfamilial or tribal groupings. Examples are in Asteraceae (Bremer, 1987, incorporating data from Jansen & Palmer, 1987) and in Faboideae (Doyle, 1987).

Systematics this century has worked through a range of phases, enlarging the spectrum of new approaches and scarcely ever relegating any as irrelevant. As a result, a valuable development has been the symposium that brings many approaches to focus on a particular large group, usually a family or an order. Apiaceae (Heywood, 1971), Asteraceae (Heywood et al., 1977), Solanaceae (Hawkes et al., 1979), Fabaceae (Polhill & Raven, 1981; Stirton, 1987), Myrtales (Raven, 1984), Poaceae (Soderstrom et al., 1987), Hamamelidae (Crane & Blackmore, 1989), and others have benefited from this treatment. Often considerable consensus has emerged but sometimes such a meeting of minds has emphasized the divergence of views, as with the status and circumscription of genera of Asteraceae (Lane & Turner, 1985).

Still wider synthesis has been the task of those who have developed systems of classification for the flowering plants as a whole. Impressive arrays of features contributed to the systems of Thorne (1981), Cronquist (1981), Dahlgren (1980; Dahlgren et al., 1985; Dahlgren & Bremer, 1985), and Takhtajan (1987). The next round of systems will differ from these by extensive use of macromolecular data.

Work has not been concentrated on the flowering plants alone. The algae have been recognized as a heterogeneous assemblage of groups. Fungi and bacteria have been more adequately divorced from green plants, and such discordant concepts as the broadly conceived pteridophytes and the gymnosperms are tending to drop from scientific usage. Homologies between major groups have been in-

vestigated and, with the increased range of morphological data available, have been the subject of cladistic studies (e.g., Bremer, 1985). The symbiotic origin of the eukaryotic cell has been a major unifying theory, now happily confirmed by the genetic homology of mitochondria with “purple bacteria” and of chloroplasts with cyanobacteria (Pace et al., 1986). The higher taxonomic levels especially can be expected to repay macromolecular studies if suitably conservative genes are chosen.

FLORAS, TENSIONS AND SYNTHESIS

This review has looked briefly at the outstanding trends over a century. But what were the taxonomists actually doing? Fortunately they were mostly not poised waiting to catch each new bandwagon as it came along. Mostly they were describing taxa, writing floras and monographs, developing the resources of collections and published work that we now have. Usually they applied only a sample of the range of available approaches to the classification of each particular plant group.

Thirty years ago Stafleu (1959) characterized the state of plant taxonomy as an “age of floras and floristic work,” noting that this was partly at the expense of synthetic and monographic studies. This characterization applies with greater force today. The increasing recognition of threats to the diversity of the biota, and also recognition of the value of that diversity, have helped taxonomists to obtain funding for large flora projects, regional, national, and international. Floras of the U.S.S.R. and Europe have been completed. Projects for Australia, China, India, North America, and South Africa have joined such longer-established works as *Flora Malesiana*, *Flora Neotropica*, *Flora of Tropical East Africa* (references in Frodin, 1984), and compilations such as Med-Checklist (Greuter et al., 1984–1989) in providing accessible information on the world’s flowering plants.

Frodin (1984) observed that so little change in style has taken place in floras over 140 years—since Torrey, Gray, Bentham, and Hooker—that “One who compares some current American state floras with Torrey’s *Flora of the State of New York* might be forgiven for thinking that the modern works had been written by descendants of Rip van Winkle”—and North America is not the only continent to which such comment applies.

Plant taxonomists are used to living in a scientific culture of some tension. Bibliographic search back more than 200 years and Latin diagnoses are still part of their stock-in-trade, although moves to change the former are being considered. Yet for

50 years intensive studies using varied techniques have competed with descriptive flora and monographic projects. Macromolecular genetics now offers involvement with aspects of one of science's fastest-moving fields. There are serious choices to be made in how much of their resources institutions and individuals should devote to their different responsibilities for flora projects, revisions, and using the most powerful tools yet available to elucidate phylogenies and thus improve classifications.

A challenge at present is to maintain cohesion in systematics across these streams so that the new developments are a scientific stimulus to the subject as a whole. Academic teachers of biology must have a broad appreciation of these approaches in research and education if the training they provide is to be relevant to the eventual careers of most research students in systematic and evolutionary biology. On the other hand, the herbaria and other institutions, while carrying the major part of most floristic projects, will need to respond positively to new developments if these organizations are to remain central to the mainstream of scientific taxonomy.

With environmental destruction and change now rampant, it was the taxonomists of these last hundred years that sampled the world's biota at the richest development it has offered for study. The immediate future gives the best chance humanity will have to investigate the diverse products and processes of evolution.

The concise flora has been an appropriate reaction to the need to record plants in regions under threat and to obtain information on diversity to support the case for conservation. This view has recently been strongly supported by Nooteboom (1988) and by Bramwell (1989). Equally, however, most macromolecular studies require access to live plants. The living collections of botanical gardens are becoming more important as research materials, just as the herbarium collections built up over the last century have become increasingly irreplaceable (Raven, 1988).

Macromolecular studies of different gene systems have commonly, but not always, given consistent results. There is particular need to investigate cases where there is disparity between results from DNA and from morphological data (Sytsma & Smith, 1988). There are instances of isozymic information on allied species corroborating morphological similarities but giving results quite at variance with comparisons of chloroplast DNA in ferns (Yatskievych & Moran, 1989) and with mitochondrial DNA in fishes (Dowling & Brown, 1989). Studies on *Lisianthus* (Gentianaceae) have given similarly discordant results (Sytsma & Schaal,

1985). It may be relevant that these apparent "failures" of DNA analysis are all applications to groups of closely allied species, whereas there has been greater success at higher taxonomic levels. As information accumulates, it may be possible to select methods appropriately to particular levels and also to interpret such discrepant findings.

Patterson (1987) postulates that "molecular homologies are no more secure, and are possibly more precarious than morphological ones," and McKenna (1987) writes, "It should also be obvious that molecular studies can suffer from exactly the same ills that beset comparative anatomical ones: a touchstone has not been found." Indeed, the succession of failed panaceas in systematics should be heeded as a warning. Nevertheless, by seeking congruence of data from different gene systems and from morphology, it appears that macromolecular methods will often produce convincing phylogenies at many taxonomic levels, and they offer a vastly expanded sample of characters.

"Reliable" taxonomies have long been contrasted with speculative phylogenies, even though the assignment of levels in taxonomic hierarchies has been accepted as partly a matter of subjective judgment. The situation is tending to be reversed.

Patterson (1987) observed that as little as 30 years ago, when phenetics was at its height, it was thought that "classification by genealogy might be a laudable goal, but not one that was attainable." In *The Origin of Species*, Darwin (1859: 486) had predicted that "Our classifications will come to be, as far as they can be so made, genealogies." To the extent that the promise of macromolecular systematics is realized, phylogenies inferred from sequence data and considered in the light of morphological and other data sources may become frameworks to use in asking important questions in other areas of biology.

If phylogenies can be accurately and reliably determined at many taxonomic levels from macromolecular information, Gottlieb (1988) is right to claim that this offers dramatic new opportunities to systematists. Human interest in organisms is not limited to their relationships, but is also in how they work as functional, adaptive systems and how genic change has been expressed in ontogeny and in phenotypes. Botanical systematics will still be an unending and widening synthesis—but on new terms.

LITERATURE CITED

- ALLAN, M. 1967. *The Hookers of Kew, 1785–1911*. Michael Joseph, London.
ALSTON, R. E. & B. L. TURNER. 1963. *Biochemical Systematics*. Prentice-Hall, Englewood Cliffs.
APPLEBY, C. A., E. S. DENNIS & W. J. PEACOCK. 1990.

- A primaevial origin for plant and animal haemoglobins? *Austral. Syst. Bot.* 3: 81–89.
- BATES, D. M., R. DAHLGREN, P. S. GREEN & K. KUBITZKI. 1980. A prospectus for a proposed new work: the families and genera of vascular plants. *Taxon* 29: 318–320.
- BAVERSTOCK, P. R. & A. M. JOHNSON. 1990. Ribosomal RNA nucleotide sequence: a comparison of newer methods used for its determination, and its use in phylogenetic analysis. *Austral. Syst. Bot.* 3: 101–110.
- BEHNKE, H.-D. 1975. The bases of angiosperm phylogeny: ultrastructure. *Ann. Missouri Bot. Gard.* 62: 647–663.
- BLUNT, W. 1978. In for a Penny—A Prospect of Kew Gardens. Hamish Hamilton, London.
- BOULTER, D. 1973. The use of amino acid sequence data in the classification of higher plants. *Nobel Symp.* 25: 211–216.
- . 1980. The evaluation of present results and future possibilities of the use of amino acid sequence data in phylogenetic studies with specific reference to plant proteins. Pp. 235–240 in F. A. Bisby et al. (editors), *Chemosystematics: Principles and Practice*. Academic Press, New York.
- BOWER, F. O. 1919. Joseph Dalton Hooker. Macmillan, New York.
- BRAMWELL, D. 1989. Taxonomy: the sands of time. *Taxon* 38: 404–405.
- BREMER, K. 1985. Summary of green plant phylogeny and classification. *Cladistics* 1: 369–385.
- . 1987. Tribal interrelationships of the Asteraceae. *Cladistics* 3: 210–253.
- BROCKWAY, L. H. 1979. Science and Colonial Expansion — the Role of the British Royal Botanic Gardens. Academic Press, New York.
- BROWN, A. H. D. 1990. The role of isozyme studies in molecular systematics. *Austral. Syst. Bot.* 3: 39–46.
- CAMIN, J. H. & R. R. SOKAL. 1965. A method for deducing branching sequences in phylogeny. *Evolution* 19: 311–326.
- CANDOLLE, A. DE. 1867. *Lois de la Nomenclature Botanique*. Massons, Paris.
- CANDOLLE, A. P. DE (editor). 1824–1874. *Prodromus systematis naturalis regni vegetabilis*. [Volumes 8–17 edited solely or jointly by A. L. de Candolle.] Treuttel & Würtz, Paris.
- CLEGG, M. T. 1989. Molecular diversity in plant populations. Pp. 89–115 in A. H. D. Brown et al. (editors), *Population Genetics, Plant Breeding and Genetic Conservation*. Sinauer Associates, Sunderland.
- , A. H. D. BROWN & P. R. WHITFIELD. 1984. Chloroplast DNA diversity in wild and cultivated barley: implications for genetic conservation. *Genet. Res.* 43: 339–343.
- CONSTANCE, L. 1964. Systematic botany—an unending synthesis. *Taxon* 13: 257–273.
- CRACRAFT, J. 1989. Review of C. Patterson (editor), *Molecules and Morphology in Evolution: Conflict or Compromise?* *Cladistics* 5: 202–210.
- CRANE, P. R. & S. BLACKMORE. 1989. *Evolution, Systematics and Fossil History of the Hamamelidae*. 2 volumes, Systematics Association Special Volume 40. Oxford University Press.
- CRAWFORD, D. J. 1983. Phylogenetic and systematic inferences from electrophoretic studies. Pp. 257–288 in S. D. Tanksley & T. J. Orton (editors), *Isozymes in Plant Genetics and Breeding, Part A*. Elsevier, Amsterdam.
- CREPET, W. L. & K. C. NIXON. 1989. Earliest megafossil evidence of Fagaceae: phylogenetic and biogeographic implications. *Amer. J. Bot.* 76: 842–855.
- CRONQUIST, A. J. 1981. *An Integrated System of Classification of Flowering Plants*. Columbia Univ. Press, New York.
- . 1987. A botanical critique of cladism. *Bot. Review* 53: 1–52.
- DAHLGREN, R. M. T. 1980. A revised system of classification of the angiosperms. *Bot. J. Linn. Soc.* 80: 91–124.
- . 1983. General aspects of angiosperm evolution and macrosystematics. *Nordic J. Bot.* 3: 119–149.
- & K. BREMER. 1985. Major clades of the angiosperms. *Cladistics* 1: 349–368.
- , H. T. CLIFFORD & P. F. YEO. 1985. *The Families of the Monocotyledons*. Springer-Verlag, Berlin.
- DARLINGTON, C. D. 1937. *Recent Advances in Cytology*, 2nd edition. Churchill, London.
- . 1939. *The Evolution of Genetic Systems*. Cambridge Univ. Press, Cambridge.
- DARWIN, C. R. 1859. *On the Origin of Species by Means of Natural Selection*. J. Murray, London.
- DAVIS, P. H. & V. H. HEYWOOD. 1963. *Principles of Angiosperm Taxonomy*. D. Van Nostrand, New York.
- DESMOND, R. G. C. 1975. The Hookers and the development of the Royal Botanic Gardens, Kew. *Biol. J. Linn. Soc.* 7: 173–182.
- DOWLING, T. E. & W. M. BROWN. 1989. Allozymes, mitochondrial DNA, and levels of phylogenetic resolution among four minnow species (*Notropis*: Cyprinidae). *Syst. Zool.* 38: 126–143.
- DOYLE, J. J. 1987. Variation at the DNA level: uses and potential in legume systematics. Pp. 1–30 in C. H. Stirton (editor), *Advances in Legume Systematics, Part 3*. Royal Botanic Gardens, Kew.
- & E. E. DICKSON. 1987. Preservation of plant samples for restriction endonuclease analysis. *Taxon* 36: 715–722.
- , J. L. DOYLE & A. H. D. BROWN. 1990. Analysis of a polyploid complex in *Glycine* with chloroplast and nuclear DNA. *Austral. Syst. Bot.* 3: 125–136.
- DUCKER, S. C. 1988. *The Contented Botanist. Letters of W. H. Harvey about Australia and the Pacific*. Melbourne Univ. Press, Melbourne.
- EHRlich, P. R. & P. H. RAVEN. 1969. Differentiation of populations. *Science* 165: 1228–1232.
- ELDRIDGE, N. & J. CRACRAFT. 1980. *Phylogenetic Patterns and the Evolutionary Process: Method and Theory in Comparative Biology*. Columbia Univ. Press, New York.
- ENGLER, H. G. A. 1892. *Syllabus der Vorlesungen über specielle und medicinisch-pharmaceutische Botanik*. Gebr. Borntraeger, Berlin.
- . 1900–1953. *Das Pflanzenreich*. Wilhelm Engelmann, Berlin.
- & K. A. E. PRANTL. 1887–1915. *Die Natürlichen Pflanzenfamilien . . .* Wilhelm Engelmann, Leipzig.
- EWAN, J. 1969. Early history. Pp. 27–48 in J. Ewan (editor), *A Short History of Botany in the United States*. Hafner, New York.
- FARRIS, J. S. 1983. The logical basis of phylogenetic

- analysis. Pp. 7-36 in N. I. Platnick & V. A. Funk (editors), *Advances in Cladistics*, Volume 2. Columbia Univ. Press, New York.
- . 1985. Distance data revisited. *Cladistics* 1: 67-85.
- FELSENSTEIN, J. 1978. Cases in which parsimony or compatibility methods will be positively misleading. *Syst. Zool.* 27: 401-410.
- FERGUSON, A. 1988. Isozyme studies and their interpretation. Pp. 184-201 in D. L. Hawkesworth (editor), *Prospects in Systematics*. Clarendon, Oxford.
- FRODIN, D. G. 1984. *Guide to Standard Floras of the World*. Cambridge Univ. Press, New York.
- GHISELIN, M. T. 1984. Narrow approaches to phylogeny: a review of nine books of cladism. *Oxford Surveys in Evol. Biol.* 1: 209-222.
- GIANNASI, D. E. & D. J. CRAWFORD. 1986. Biochemical systematics II. A reprise. Pp. 25-248 in M. K. Hecht, B. Wallace & G. T. Prance (editors), *Evolutionary Biology*, Volume 20. Plenum Press, New York.
- GOTTLIEB, L. D. 1984. Isozyme evidence and problem solving in plant systematics. Pp. 343-357 in W. F. Grant (editor), *Plant Biosystematics*. Academic Press, Canada.
- . 1988. Towards molecular genetics in *Clarkia*: gene duplications and molecular characterization of PGI genes. *Ann. Missouri Bot. Gard.* 75: 1169-1179.
- GRANT, V. 1981. *Plant Speciation*, 2nd edition. Columbia Univ. Press, New York.
- GRANT, W. F. (editor). 1984. *Plant Biosystematics*. Academic Press, Canada.
- GRAY, J. L. 1893. *Letters of Asa Gray*, 2 volumes. Houghton Mifflin, Boston. [Reprinted Franklin, New York.]
- GREUTER, W., H. M. BURDET & G. LONG. 1984-1989. *Med-Checklist. Cons. et Jard. Botan.: Genève*.
- HAMBY, R. K. & E. A. ZIMMER. 1988. Ribosomal RNA sequences for inferring phylogeny within the grass family (Poaceae). *Pl. Syst. Evol.* 160: 29-37.
- HARBORNE, J. B. & B. L. TURNER. 1984. *Plant Chemotaxonomy*. Academic Press, Orlando, Florida.
- HAWKES, J. G., R. N. LESTER & A. D. SKELDING. 1979. *The Biology and Taxonomy of the Solanaceae*. Academic Press, London.
- HAUFLER, C. H. 1989. Species concepts in pteridophytes: summary and synthesis. *Amer. Fern. J.* 79: 90-93.
- HEGNAUER, R. 1962-1973. *Chemotaxonomie der Pflanzen*, 6 volumes. Birkhäuser Verlag, Basel & Stuttgart.
- HEISER, C. B. 1969. Taxonomy. Pp. 110-114 in J. Ewan (editor), *A Short History of Botany in the United States*. Hafner, New York.
- HENNIG, W. 1950. *Grundzüge einer Theorie der Phylogenetischen Systematik*. Deutscher Zentralverlag, Berlin.
- . 1966. *Phylogenetic Systematics*. Univ. Illinois Press, Urbana.
- HEPPER, F. N. 1982. *Kew—Gardens for Science and Pleasure*. H. M. Stationery Office, London.
- HEYWOOD, V. H. (editor). 1971. *The Biology and Chemistry of the Umbelliferae*. Academic Press, London.
- , J. B. HARBORNE & B. L. TURNER (editors). 1977. *The Biology & Chemistry of the Compositae*. Academic Press, London.
- HICKEY, L. J. & J. A. WOLFE. 1975. The bases of angiosperm phylogeny: vegetative morphology. *Ann. Missouri Bot. Gard.* 62: 538-589.
- HOOKE, J. D. 1859. Introductory essay. In: *The Botany of the Antarctic Voyage of H. M. Discovery Ships 'Erebus' and 'Terror' in the Years 1839-1843, III. Flora Tasmaniae*. Lovell Reeve, London.
- HULL, D. L. 1988. *Science as a Process*. Univ. Chicago Press, Chicago.
- HUMPHREY, H. B. 1961. *Makers of North American Botany*. Ronald Press, New York.
- JACKSON, B. D. 1906. *George Bentham*. Dent, London.
- JANSEN, R. K. & J. D. PALMER. 1987. A chloroplast DNA inversion marks an ancient evolutionary split in the sunflower family (Asteraceae). *Proc. Natl. Acad. U.S.A.* 84: 5818-5822.
- & ———. 1988. Phylogenetic implications of chloroplast DNA restriction site variation in the Mutisieae (Asteraceae). *Amer. J. Bot.* 75: 751-764.
- , ——— & H. J. MICHAELS. 1988. Investigations of chloroplast DNA variation in the Asteraceae. *Comp. Newsl.* 15: 2-11.
- JOHNSON, L. A. S. 1968, 1970. Rainbow's end: the quest for an optimal taxonomy. *Proc. Linn. Soc. New South Wales* 93: 7-45 (1968). [Reprinted (with Addendum) in *Syst. Zool.* 19: 203-239. (1970).]
- . 1989. Models and reality: doctrine and practicality in classification. *Pl. Syst. Evol.* 168: 95-108.
- & B. G. BRIGGS. 1975. On the Proteaceae—the evolution and classification of a southern family. *Bot. J. Linn. Soc.* 70: 83-182.
- & ———. 1984. Myrtales and Myrtaceae—a phylogenetic analysis. *Ann. Missouri Bot. Gard.* 71: 700-756.
- JORGENSEN, R. A. & P. D. CLUSTER. 1988. Modes and tempos in the evolution of nuclear ribosomal DNA: new characters for evolutionary studies and new markers for genetic and population studies. *Ann. Missouri Bot. Gard.* 75: 1238-1247.
- KALKMAN, C. 1988. The phylogeny of the Rosaceae. *Bot. J. Linn. Soc.* 98: 37-59.
- KING, R. 1985. Royal Kew. Constable, London.
- LANE, M. A. & B. L. TURNER (editors). 1985. The generic concept in the Compositae: a symposium. *Taxon* 34: 5-88.
- MA, W. L. 1988. The historic and current status of herbaria in China. *Taxon* 37: 870-875.
- MARTIN, P. G. & J. M. DOWD. 1990. A protein sequence study of the dicotyledons and its relevance to the evolution of the legumes and nitrogen fixation. *Austral. Syst. Bot.* 3: 91-100.
- MAYR, E. 1965. Numerical phenetics and taxonomic theory. *Syst. Zool.* 14: 73-97.
- MCKENNA, M. C. 1987. Molecular and morphological analysis of high-level mammalian interrelationships. Pp. 55-93 in C. Patterson (editor), *Molecules and Morphology in Evolution: Conflict or Compromise?* Cambridge Univ. Press, Cambridge.
- MELCHIOR, H. 1964. *A. Engler's Syllabus der Pflanzenfamilien*, 12th edition, Volume 2. Angiospermen. Borntraeger, Berlin.
- MOORE, D. M. 1978. The chromosomes and plant taxonomy. Pp. 39-56 in H. E. Street (editor), *Essays in Plant Taxonomy*. Academic Press, London.
- NEIGEL, J. E. & J. C. AVISE. 1986. Phylogenetic mitochondrial DNA under various demographic models of speciation. Pp. 515-534 in S. Karlin & E. Nevo

- (editors), *Evolutionary Processes and Theory*. Academic Press, Orlando, Florida.
- NELSON, G. & N. I. PLATNICK. 1981. *Systematics and Biogeography: Cladistics and Vicariance*. Columbia Univ. Press, New York.
- NOOTEBOOM, H. P. 1988. What should botanists do with their time? *Taxon* 37: 134.
- PAABO, S. 1989. Ancient DNA: extraction, characterization, molecular cloning, and enzymatic amplification. *Proc. Natl. Acad. U.S.A.* 86: 1939-1943.
- PACE, N. R., G. J. OLSEN & C. R. WOESE. 1986. Ribosomal RNA phylogeny and the primary lines of evolutionary descent. *Cell* 45: 325-326.
- PALMER, J. D. 1987. Chloroplast DNA evolution and biosystematic uses of chloroplast DNA variation. *Amer. Naturalist* 130, S6-S29.
- , R. K. JANSEN, H. J. MICHAELS, M. W. CHASE & J. R. MANHART. 1988. Chloroplast DNA variation and plant phylogeny. *Ann. Missouri Bot. Gard.* 75: 1180-1206.
- PATTERSON, C. 1987. Introduction. Pp. 1-22 in C. Patterson (editor), *Molecules and Morphology in Evolution: Conflict or Compromise?* Cambridge Univ. Press, Cambridge.
- PENNY, D., M. D. HENDY & I. M. HENDERSON. 1987. Reliability of evolutionary trees. *Cold Spring Harbour Symposium on Quantitative Biology* 52: 857-862.
- , ———, E. A. ZIMMER & R. K. HAMBY. 1990. Trees from sequences: panacea or Pandora's box? *Austral. Syst. Bot.* 3: 21-38.
- POLHILL, R. M. & P. H. RAVEN (editors). 1981. *Advances in Legume Systematics, Parts 1 & 2*. Royal Botanic Gardens, Kew.
- & J. E. VIDAL. 1981. Tribe 1. Caesalpinieae. Pp. 81-95 in R. M. Polhill & P. H. Raven (editors), *Advances in Legume Systematics, Part 1*. Royal Botanic Gardens, Kew.
- RANKER, T. A. & C. R. WERTH. 1986. Active enzymes from herbarium specimens: electrophoresis as an afterthought. *Amer. Fern. J.* 76: 102-113.
- RAVEN, P. H. 1975. The bases of angiosperm phylogeny: cytology. *Ann. Missouri Bot. Gard.* 62: 724-764.
- . 1976. Systematics and plant population biology. *Syst. Bot.* 1: 284-316.
- . 1977. The systematics and evolution of higher plants. Pp. 59-83 in C. E. Goulden (editor), *The Changing Scene in Natural Sciences, 1776-1976*. Academy of Natural Sciences, Philadelphia, Spec. Publ. 12, Lancaster.
- . 1980. Hybridization and the nature of species in higher plants. *Canad. Bot. Assoc. Bull., Suppl.* to 13: 3-10.
- (editor). 1984. The order Myrtales: a symposium. *Ann. Missouri Bot. Gard.* 71: 631-985.
- . 1986. Modern aspects of the biological species in plants. Pp. 11-29 in K. Iwatsuki, P. H. Raven & W. J. Bock (editors), *Modern Aspects of Species*. Univ. Tokyo Press, Tokyo.
- . 1988. The issue of conservation in natural history museums. P. 12 in *Abstracts from the 1988 Annual Meeting, Society for Preservation of Natural History Collections*. Carnegie Mus. Nat. Hist., Pittsburgh, Pennsylvania.
- RITLAND, K. & M. T. CLEGG. 1987. Evolutionary analysis of plant DNA sequences. *Amer. Naturalist* 130, S74-S100.
- ROLLINS, R. C. 1965. The role of the university herbarium in research and teaching. *Taxon* 14: 115-120.
- SCOURSE, N. 1983. *The Victorians and their Flowers*. Croom Helm, London.
- SMALL, E. 1989. Systematics of biological systematics (or, Taxonomy of taxonomy). *Taxon* 38: 335-356.
- SNEATH, P. H. A. & R. R. SOKAL. 1973. *Numerical Taxonomy*. W. H. Freeman, San Francisco.
- SODERSTROM, T. R., K. W. HILU, C. S. CAMPBELL & M. E. BARKWORTH (editors). 1987. *Grass Systematics and Evolution*. Smithsonian Inst. Press, Washington, D.C.
- SOKAL, R. R. & P. H. A. SNEATH. 1963. *The Principles of Numerical Taxonomy*. W. H. Freeman, San Francisco.
- STAFLEU, F. A. 1959. The present status of plant taxonomy. *Syst. Zool.* 8: 59-68.
- . 1966. The great Prodrômus. In: A. P. de Candolle, *Prodrômus systematis naturalis regni vegetabilis, 1823-1873*, reprint of volumes 1-8: 5-41. J. Cramer, Lehre (FRG).
- . 1972. The volumes on cryptogams of "Engler und Prantl." *Taxon* 21: 501-511.
- . 1988. The prehistory and history IAPT. *Taxon* 37: 791-800.
- [STAPF, O.] (AS 'O. S.'). 1930. Adolf Engler [obituary]. *Bull. Misc. Inform.* 10: 495-498.
- STEBBINS, G. L. 1950. *Variation and Evolution in Plants*. Columbia Univ. Press, New York.
- STEVENS, P. F. 1984. Metaphors and typology in the development of botanical systematics 1690-1960, or the art of putting new wine in old bottles. *Taxon* 33: 169-211.
- STIRTON, C. H. 1987. *Advances in Legume Systematics, Part 3*. Royal Botanic Gardens, Kew.
- SWOFFORD, D. L. 1985. *PAUP, Phylogenetic Analysis Using Parsimony, Version 2.3*. Illinois Natural History Survey Program Manual, Urbana, Illinois.
- SYTSMA, K. J. & B. A. SCHAAL. 1985. Phylogenetics of the *Lisianthus skinneri* (Gentianaceae) species complex in Panama utilising DNA restriction fragment analysis. *Evolution* 39: 594-608.
- & J. F. SMITH. 1988. DNA and morphology: comparisons in the Onagraceae. *Ann. Missouri Bot. Gard.* 75: 1217-1237.
- TAKHTAJAN, A. 1987. *Sistema Magnoliifitov [Systema Magnoliophytorum]*. Izdatel'stvo "Nauka," Leningrad.
- TATON, R. (editor). 1965. *Science in the Nineteenth Century*. (Translated by A. J. Pomerans.) Thames & Hudson, London.
- TEMPLETON, A. R. 1983. Phylogenetic inference from restriction endonuclease cleavage site maps with particular reference to the evolution of humans and the apes. *Evolution* 37: 221-244.
- THORNE, R. F. 1981. Phytochemistry and angiosperm phylogeny: a summary statement. Pp. 233-295 in D. Young & D. Seigler (editors), *Phytochemistry and Angiosperm Phylogeny*. Praeger Scientific, New York.
- TORREY, J. & A. GRAY. 1838-1843. *A Flora of North America*, 2 volumes. Wiley & Putnam, New York.
- VICKERY, R. K. 1984. Biosystematics 1983. Pp. 1-24 in W. F. Grant (editor), *Plant Biosystematics*. Academic Press, Canada.
- WAGNER, W. H., JR. 1961. Problems in the classification of ferns. Pp. 841-844 in D. L. Bailey (editor),

- Recent Advances in Botany, Volume 1. Univ. Toronto Press, Toronto.
- WALKER, J. W. ET AL. 1975. The bases of angiosperm phylogeny. *Ann. Missouri Bot. Gard.* 62: 515–834.
- WILEY, E. O. 1981. *The Theory and Practice of Phylogenetic Systematics*. Wiley-Interscience, New York.
- WILLIS, M. 1949. *By Their Fruits—A Life of Ferdinand von Mueller*. Angus & Robertson, Sydney.
- YATSKIEVYCH, G. & R. C. MORAN. 1989. Primary divergence and species concepts in ferns. *Amer. Fern J.* 79: 36–45.
- ZURAWSKI, G. & M. T. CLEGG. 1987. Evolution of higher-plant chloroplast DNA-encoded genes: implications for structure-function and phylogenetic studies. *Annual Rev. Pl. Physiol.* 38: 391–418.